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INHERITANCE OF WHITE-SPOTTING AND OTHER COLOR CHARACTERS IN CATS

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IN a previous paper[1] I have presented data bearing on the general subject of the inheritance of coat-color in cats. The experiments at the University of Pennsylvania were still in progress when the paper was published and further results have since been obtained. Unfortunately an eczema infected the stock and the investigations were brought to an end by the death of several animals. It is thought advisable therefore to present the rest of the data in the present paper and to summarize results thus far obtained.

Numbers denoting individuals or matings are inserted as in the previous paper for the purpose of cross reference. In the genetic formulæ A' denotes much-ticked; A, little-ticked; a, non-ticked; B' denotes lined; B, striped; b, blotched; M, denotes intensely pigmented; m, maltese dilution; W denotes dominant solid white; w, color; Y denotes yellow; y, black; Yy, tortoiseshell. Symbols are omitted when character was for any reason undetermined.

A cream male (24) (b.m.w.Y) was crossed (48) to a solid-white yellow-eyed half sister (29) (W) from mating 43 (a white male by an "anomalous" (Yy) cream female (23) mentioned below). There were produced one orange male (b.M.w.Y), and one cream female (b.m.w.Y). Both

[1] Whiting, P. W., "Inheritance of Coat-Color in Cats," *The Journal of Experimental Zoology*, Vol. 25, No. 2, April, 1918.

had an extreme amount of white-spotting. The same male (24), when crossed (51) to his "anomalous" (Yy) cream mother, (23) (b.m.w.Yy), sired two cream females (b.m.w.Y). He was also crossed (53) to a black female, (32) (a.B.M), and sired one maltese male, (a.B.m.w.y) and four tortoiseshell females, (one a.B.M, one b.m, and two a.M).

The progeny from the "anomalous" (Yy) cream female (23) by her cream son (24) now consists of four litters (41, 46, 50, and 51) containing two maltese males (yX —), one cream male (YX —) and four cream females (YX ?X).

There are now in all eight matings of "yellow" male (YX —) by "black" female (yX yX) giving sixteen "black" males (yX —) and seventeen "tortoiseshell" females (YX yX).

Dr. Charles Penrose, of Philadelphia, very kindly loaned his Caffer cat for crossing, a much-ticked lined male (21) (A′.B′.M.y) mentioned in the previous paper. A cross (52) made with an orange striped female (31) (B.M.Y), from mating 37 produced three tortoiseshell females,—a much-ticked lined (A′.B′.M.Yy), a lined with ticking present but with so much yellow that the exact degree was uncertain, (B′.M.Yy), a ticked of uncertain degree in which the banding was also uncertain on account of admixture of black and yellow, (M.Yy).

The same male (21), crossed (55) to an orange striped sister (33) (B.M.Y) of female 31, sired five orange lined males (B′.M.Y).

The same male (21) crossed (54) to a tortoiseshell (28) (a.B.M.Yy) sired four lined non-yellow kittens,—two little-ticked males (A.B′.M.y), and two much-ticked females (A′.B′.M.y).

The same male (21) crossed (56) to a blotched maltese tortoiseshell (13) (A.b.m.Yy) sired four lined orange males (B′.M.Y) and two lined tortoiseshell females (B′.M.Yy).

When he was crossed (57) to a dilute tortoiseshell (34)

(a.b.m.yY), there were produced a lined orange male (B′M.Y) and a lined tortoiseshell female (B′.M.Yy).

When he was crossed (58) to a tortoiseshell female (30) (a.B.M.Yy) he sired two orange lined males (B′.M.Y), one little-ticked, lined male (A.B′.M.y), and two lined females,—one tortoiseshell with so much yellow that degree of ticking could not be made out (B′.M.Yy), and one non-yellow with so much white that degree of ticking could not be made out (B′.M.y).

The crosses of this Caffer cat are reciprocal to those summarized above, crosses of "yellow" males (YX —) by "black" (yX yX) and by "tortoiseshell" (YX yX) females. Here we have a "black" male (yX —) by "yellow" females (YX YX) giving five "yellow" males (YX —) and three "tortoiseshell" females (YX yX) and a "black" male (yX —) by "tortoiseshell" females (YX yX) giving three "black" males (yX —) and seven "yellow" males (YX —) and four "tortoiseshell" females (YX yX) and three "black" females (yX yX). It may be seen, therefore, that the principle of sex-linkage applies in all these cases.

The progeny of the Caffer cat (21) are of interest also from the point of view of ticking and banding. The essential characteristic of Caffer is the narrow banded or "lined" condition. Banding of intermediate width, "striping," acts as a recessive as previously shown and the widest bands, "blotches," are recessive to both "lines" and "stripes." The parents (18, 19) of this cat were both lined, but produced blotched offspring as well as lined. Evidently this cat (21) is the homozygous segregate, for twenty-four of his twenty-five offspring are certainly lined and in the other (52.3) there is so much white-spotting and so much intermixture of yellow and black in the pigmented areas that the condition of banding is uncertain. It is probable, however, that even in this case a wider type of bands,—stripes or blotches, would have been more easily seen. Of the females to which cat 21 was crossed, two (13, 34) were blotched, and

the other four (28, 30, 31, 33) were striped but known to be carrying blotched. Lined is therefore dominant to both striped and blotched as previously stated. The results thus far obtained do not demonstrate the allelomorphism of the three types of banding. In order to do that it would be necessary to cross one of the offspring carrying striped (B'B) to blotched cats (bb). All kittens should be lined (B'b) or striped (Bb). If blotched occurred it would demonstrate that two loci were involved, Ll and Ss. Blotched would then be ll.ss, and the nomenclature would have to be changed.

The production of orange and tortoiseshell lined cats is of interest. They are as expected in every way comparable to other oranges and tortoiseshells except for the narrower bands.

Results in regard to ticking may now be considered. In the previous paper *a* was used to denote lack of ticking; *A*, little-ticked or dark tabby; and *A'*, much-ticked or light tabby. It now appears that there are two hereditary grades of ticking previously grouped under *A'* between which there is a fairly wide difference. Comparison of kittens at birth or of adult cats makes the distinction clear. During growth intergradations appear for ticking increases with age as in rodents. *A'* should therefore be divided into A^e, extreme-ticking, and A^m, much-ticking. Fully as much difference exists between A^e and A^m as between A^m and *A*.

A blotched male (11) crossed (14) with a black female (15) sired four blotched kittens, and a blotched female (14) crossed (31) with a lined little-ticked male (18) produced one lined and three blotched offspring. The two blotched cats (11 and 14) were extremely-ticked, A^e, as were also the eight kittens. A much-ticked, A^m, Caffer female (19) when crossed (19) to the little-ticked, *A*, Caffer male (18) produced one much-ticked (21) and three little-ticked. The much-ticked mother (19) and son (21) are very similar and contrast strongly with the extremely-ticked cats mentioned as well as with little-

ticked. With the exception of five kittens, the offspring of the much-ticked male (21) are useless for determining degree of ticking on account of the presence of yellow. Three kittens (58.2, 54.3, and 54.4) are little-ticked like their grandfather (18). Two kittens (54.1, 54.2) were much-ticked like their father and grandmother. The mothers of all of these kittens were non-ticked. The same degrees of ticking, A^m and A, have been possessed by three generations.

Skins illustrating the three types of ticking A^c, A^m, and A are preserved for reference.

The crosses summarized in the preceding paper and above may now be considered from the point of view of white-spotting. Solid-white acts as a complete dominant to other colors as shown in the previous paper. White-spotting as seen among cats in general grades all the way from solid-white to self. In individual fraternities, however, it may show wide and clean segregation as the crosses below demonstrate. A "self" cat may have a *minute* white spot on breast of belly or a few sparsely scattered white hairs. In this case it might be called near-self. Restricted spotting denotes white on nose, breast, belly, or feet. It segregates widely from near-self in the crosses here considered, but grades into moderate spotting, which denotes the further extension of white to sides of body as well. Moderate spotting in turn grades into considerable, which denotes more white than color. Extreme spotting denotes that pigment is limited to small spots on head, back, or tail.

Crosses involving only self, restricted and moderate spotting, and solid-white may be considered first.

A self male (18) crossed (19, 31) to two self females (19, 14) sired eight self. One of these self offspring (21) crossed (55) to a self female (33) sired five self. Self *may* therefore breed true.

The first mentioned self male (18) crossed (28, 29) with two restricted spot females (10, 2) sired three self and four restricted spot. The other self male (21)

crossed (54, 56) to two restricted spot females (28, 13) sired five self and five restricted spot. A restricted spot male (8) crossed twice (9, 30) to a self female (20) sired three self and seven restricted spot. A restricted spot female (3) crossed (16) to a self male (6) produced six self. Self by restricted spot therefore has produced seventeen self and sixteen restricted spot, the expectation if restricted spot is heterozygous.

The restricted spot male (8) crossed (12, 33) to two restricted spot females (25, 3) sired one self, three restricted, and one moderate. This is in line with expectation if spotting is dominant, the moderate in this case possibly representing the homozygote.

The same restricted spot male (8) crossed (32) to a solid-white (22) sired two solid-white and two completely self. This is in line with the assumption that the white female was homozygous for self, *ss,* and heterozygous for color, *Ww,* or that spotting and white are both allelomorphic with self and that she was carrying self. The male would then be w^1w, w^1 standing for restricted or moderate spotting.

Crosses involving greater amounts of spotting may now be considered.

The self male (21) crossed (52) to a considerable spot female (31) sired one self and two considerable. When crossed (58) to a moderate spot (30) he sired three self and two considerable. These results show that considerable segregates from self and that a greater degree of spotting may be produced from a less by crossing to self. Modifiers are indicated.

The same male was also crossed (57) to a considerable (34) and sired two restricted. In this case modifiers may have been assorted to produce restriction, but the female (34) was derived from a cross (34) of a considerable (24) by a restricted (3) each of which was known to carry self. She may therefore have been of composition $w^m w^1$; w^m, much spotting, being derived from her considerable parent and w^1, little spotting, from her re-

stricted parent. She could then produce restricted offspring, w^1w, when crossed to self.

Offspring of self by spotted known to carry self are therefore twenty-one self and twenty spotted.

The considerable spot male (24) was crossed to various spotted females known by these or other crosses to produce self. With a restricted (3) he sired (34, 49) two self, one restricted, three moderate, and three considerable. With a moderate (32) he sired (53) two self, one restricted, one moderate and one extreme. With a restricted (28) he sired (44) one self, one restricted, one moderate, and one considerable. With a moderate (30) he sired (45) two considerable and one extreme. With a restricted (13) he sired (47) two self, two considerable (one of which graded toward extreme), and one very extreme. This last cross is interesting for the offspring vary far in both directions from the parental types.

Crosses of spotted by spotted when both carry self have produced twenty-three spotted to eight self which is very close to the three-to-one expectation.

The considerable spot male (24) above mentioned when crossed (41, 46, 50, 51) to his considerable spot mother (23) sired five considerable and two restricted, the segregation being striking through failure of any moderates to appear. This is in line with the supposition that the mother (23) was carrying little spotting and was therefore of composition w^mw^1. The cross might therefore be $w^mw \times w^mw^1 = 5(w^mw^m, w^mw \text{ or } w^mw^1) + 2(w^1w)$.

The same male (24) (w^mw) was crossed (48) to a solid-white half sister (29) from the same mother (23) (w^mw^1) by a white male ($W?$). There were produced two extreme spot. The white female (29) may therefore have been Ww^m and the extreme spot offspring w^mw^m.

The failure of anything higher than restricted spotting to occur among the offspring of restricted by self, although cats with considerable may carry self, indicates that there may be allelomorphic factors determining different degrees of spotting. In any case it appears

that self is recessive to spotting and that color is recessive to solid-white. The principle is suggested that there is a quadruple allelomorphic series:—*W*, solid-white; w^m, much spotted; w^1, little spotted; and *w*, self, with dominance in the degree of decreasing pigmentation. Crosses of white to self and of spotted to self would be of value in checking this principle. Any one white cat might throw besides white *either* much spotted, little spotted, *or* self; a much spotted might throw besides much, *either* little *or* self, and little should throw little or little and self. If three distinct types were produced from any one white or spotted cat crossed to numerous self cats, this would demonstrate modifiers of considerable importance or disprove the hypothesis of allelomorphism suggested.

Attention should be called to an interesting but unexplained relation that exists between yellow- and white-spotting. "Self" tortoiseshells have yellow hairs closely intermixed with non-yellow. This makes it very difficult to determine degree of ticking in such animals. Tortoiseshells with restricted white-spotting tend to have yellow separated into patches, while further extension of white separates yellow and non-yellow areas still more. Separation of yellow into patches appears not to be correlated with amount of yellow.

GENERAL SUMMARY OF INHERITANCE OF COAT-COLOR IN CATS

It may be of interest to summarize very briefly the genetic data thus far collected on coat-color in cats. Ratios are not significant since fraternities from homozygous dominants and heterozygotes are included together.

Maltese dilution, *m*, is presumably a simple recessive to intensity, *M*. Intense by intense have produced 41 intense. Intense by dilute have produced 37 intense and 23 dilute. Dilute by dilute have produced 18 dilute.

Solid-white, *W*, evidently acts as a simple dominant

over color, *w*. It is true-breeding in the hands of fanciers. White by color (amount of white-spotting undetermined) have produced 3 white and 4 colored (one near-self). Table I shows summaries for white and white-spotting of determined degree. It is obvious that although exten-

TABLE I

Parents.	Offspring					
	Solid White, *W*	Extreme Spotting, *E*	Considerable Spotting, *C*	Moderate Spotting *M*	Restricted Spotting, *R*	Self or Near-Self, *S*
W×W	3					1
W×C	1	2				
W×R	7					2
C×C			5		2	
C×M		2	2	1	1	2
C×R		1	6	4	2	5
R×R				1	3	1
Spotted×spotted		3	13	6	8	8
C×S			2		2	1
M×S			2			3
R×S					16	17
Spotted × self			4		18	21
S×S						13

sively pigmented animals appear among the offspring of cats showing much white there is little tendency for a kitten to show more white than appears in either parent.

Table II gives a summary of the results thus far col-

TABLE II

Parents	Offspring					
	Black		Yellow		Tortoiseshell	
	♂	♀	♂	♀	♂	♀
Yellow ♂ × black ♀ Doncaster	51	*13*			*1*	51
Whiting	16					17
Total	67	*13*			*1*	68
Black ♂ × yellow ♀ Doncaster			20			16
Whiting			5			3
Total			25			19
Yellow ♂ × tortoiseshell ♀ Doncaster	45	*6*	58	53	*1*	45
Whiting	3		3	4		4
Total	48	*6*	61	57	*1*	49
Black ♂ × tortoiseshell ♀ Doncaster	32	15	37		*1*	21
Whiting	3	3	7			4
Total	35	18	44		*1*	25
Yellow ♂ × yellow ♀ Doncaster			48	40		*3* from one pair
Yellow ♂ × yellow ♀ no. 23	*3*		1	4		*1*
Black ♂ × yellow ♀ no. 23	*2*	*1*	2			2

lected in reference to the inheritance of yellow. Doncaster's[2] summaries from fancy breeders and from Little's data are given, kittens of undetermined sex being omitted. The three tortoiseshell females from one pair of Doncaster's yellow by yellow may be readily explained if it be supposed that the mother was an extreme yellow variant of the heterozygote *Yy*, comparable with my cream female number 23. Anomalous black females may be similarly heterozygous. Anomalous blacks and tortoiseshells are to be expected from anomalous yellow females. Anomalous offspring are recorded in italics in Table II.

As regards banding, certain creams and blacks could not be classified and are consequently omitted from the summaries. Lined by lined have given 2 lined and 2 blotched. Lined by striped have given 17 lined and 2 striped. Lined by blotched have given 12 lined and 4 blotched. Striped by blotched have given 19 striped and 8 blotched. Blotched by blotched have given 4 blotched.

As regards ticking, it is necessary to omit all yellows and many tortoiseshells, as well as some with much white. Extremely-ticked by little-ticked have given 4 extremely-ticked. Extremely-ticked by black have given 4 extremely-ticked. Much-ticked by little-ticked have given 1 much-ticked and 3 little-ticked. Much-ticked by black have given 2 much-ticked and 3 little-ticked. Little-ticked by little-ticked have given 5 little-ticked and 1 black. Little-ticked by black have given 7 little-ticked.

[2] Doncaster, L., "On Sex-limited Inheritance in Cats, and Its Bearing on the Sex-limited Transmission of Certain Human Abnormalities," *Journal of Genetics*, June, 1913.